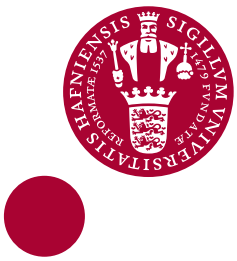

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RESEARCH ARTICLE

Drivers of plant traits that allow survival in wetlands

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Abstract

1. Plants have developed a suite of traits to survive the anaerobic and anoxic soil conditions in wetlands. Previous studies on wetland plant adaptive traits have focused mainly on physiological aspects under experimental conditions, or compared the trait expression of the local species pool. Thus, a comprehensive analysis of potential factors driving wetland plant adaptive traits under natural environmental conditions is still missing.
2. In this study, we analysed three important wetland adaptive traits, that is root porosity, root/shoot ratio and underwater photosynthetic rate, to explore driving factors using a newly compiled dataset of wetland plants. Based on 21 studies at 38 sites across different biomes, we found that root porosity was affected by an interaction of temperature and hydrological regime; root:shoot ratio was affected by temperature, precipitation and habitat type; and underwater photosynthetic rate was affected by precipitation and life-form. This suggests that a variety of driving mechanisms affect the expression of different adaptive traits.
3. The quantitative relationships we observed between the adaptive traits and their driving factors will be a useful reference for future global methane and denitrification modelling studies. Our results also stress that besides the traditionally emphasized hydrological driving factors, other factors at several spatial scales should also be taken into consideration in the context of future functional wetland ecology.

KEYWORDS

adaptive strategy, bioclimatic variables, driving factors, root porosity, root/shoot ratio, underwater photosynthetic rate, wetland plant ecophysiological adaptive traits, wetland plant functional traits

1 | INTRODUCTION

Wetland ecosystems are of global importance for their provisioning of ecosystem services such as flood abatement, habitat provision, water purification and carbon sequestration at the regional and global scale (Zedler & Kercher, 2005). Among the variety of global wetland ecosystems (Ramsar Convention Secretariat, 2013), peat-forming wetlands (including bogs, fens and swamps) alone are considered to store more than half the amount of carbon present in the atmosphere (Page & Baird, 2016). At the same time, wetlands are the dominant single global methane emission source, contributing some 20%–40% of global methane emissions (Ringeval et al., 2010). To help understand these wetland functions, plant functional traits can be used to link the environmental conditions and species composition to the ecosystem processes (Moor et al., 2017). Unravelling these inter-linkages at a global scale is essential to inform ecological modelling, such as dynamic global vegetation models (DGVMs), to improve our predictions on important processes such as global wetland methane emissions (Miller et al., 2016; Wania et al., 2013).

Wetland ecosystems are distinguished from other (non-wetland) terrestrial ecosystems by their unique hydrological and anoxic soil conditions and associated biogeochemical processes. To survive in wetlands, plants need to deal with the lack of oxygen in the rooting substrate to avoid cellular energy deficits and the potential accumulation of phytotoxic compounds. Oxygen depletion in tissues can also lead to an accumulation of reactive oxygen species upon return to aerobic conditions after flooding, causing damage to cellular macromolecules and membranes (Bailey-Serres & Voesenek, 2008; Colmer & Voesenek, 2009; Yordanova, Christov, & Popova, 2004). In the rhizosphere, the lack of oxygen as an electron acceptor results in the production of toxic chemical matter such as ferrous iron and sulphide (Singer & Havill, 1993) and low-weight monocarboxylic acids (e.g. acetic, propionic, butyric and hexanoic acids) which impair plant root function (Armstrong & Armstrong, 2001; Pezeshki, 2001). There are also environmental stressors that are specific to a certain wetland type, such as salinity in saline wetlands (Flowers & Colmer, 2008). In this study, we focus on generalities that apply to all wetlands.

To cope with these adverse conditions, wetland plants have developed a suite of adaptive traits (Pan, Cieraad, & van Bodegom, 2019; Voesenek, Colmer, Pierik, Millenaar, & Peeters, 2006; Winkel et al., 2016). Examples of adaptive traits include the following: enhanced shoot and root porosity (aerenchyma formation) to facilitate internal oxygen transportation, ameliorate oxygen concentration in the root zone and aid (root) respiration and oxidation (Colmer, 2003b; Mcdonald, Galwey, & Colmer, 2001; Visser, Colmer, Blom, & Voesenek, 2000); shoot elongation to allow leaves to access atmospheric oxygen; decreased root/shoot ratios to create a better balance between gas transport capacity (oxygen source) and root oxygen consumption (oxygen sink; van Bodegom, Kanter, Bakker, & Aerts, 2005; Jung, Hoffmann, & Muller, 2009); and a root radial oxygen loss (ROL) barrier to reduce diffusion of precious oxygen to the rhizosphere (Armstrong, Cousins, Armstrong, Turner, & Beckett, 2000; Colmer, 2003a). Underwater photosynthesis is an important process for growth and long-term persistence of wetland plants under submerged conditions, which create low HCO_3^-/CO_2 concentrations and low light intensity (Colmer, Winkel, & Pedersen, 2011; Mommer & Visser, 2005; Pedersen, Colmer, Borum, Zavala-Perez, & Kendrick, 2016; Pedersen, Vos, & Colmer, 2006). Adaptive traits involved in maintaining an optimal underwater photosynthetic rate include gas film formation (Colmer & Pedersen, 2008), changed leaf morphological structure to become thinner, narrower, with reduced cuticles and rearranged chloroplasts closer to the epidermis (Konnerup & Pedersen, 2017; Voesenek et al., 2006).

The expression of wetland adaptive traits is likely determined by bioclimatic variables, hydrological regime, habitat type and plant life-form. Bioclimatic variables (e.g. precipitation, temperature) may affect fundamental ecophysiological processes such as enzymatic activities and transpiration rates (Moles et al., 2014) that may also be important in wetlands. However, these driving forces may be different than that in terrestrial systems, for example in relation to the general lack of water limitation in wetlands compared with terrestrial plants. The hydrological regime, that is both the duration and depth of the water-table (e.g. waterlogged or submerged), has a direct impact on wetland conditions and plant performance, and is recognized as an important factor. However, its importance in comparison to other drivers, such as habitat type or bioclimatic variables, is unknown. Habitat type (e.g. marsh or floodplain) may drive the adaptive traits, for example through specific soil biochemistry, flooding depth (Voesenek, Rijnders, Peeters, van de Steeg, & de Kroon, 2004) or competition/facilitation of the local plant community (Luo, Xie, Chen, Li, & Qin, 2010; Maestre, Callaway, Valladares, & Lortie, 2009). Plant life-form (such as sedge, grass, floating-leaved) in turn reflects plant morphological characteristics and life-history strategies, and therefore might constrain the upper and lower range of adaptive traits. Our understanding of driving factors is further hampered by the often complex interactions among driving forces of plant functional traits in wetlands (Moor et al., 2017). For instance, while the temperature in shallow waterbodies can fluctuate markedly, affecting the rate of underwater photosynthesis of tropical seagrass (Pedersen et al., 2016), deeper waterbodies is much more stable even with strong changes in the surrounding air temperature (Colmer et al., 2011). Likewise, the impact of a low redox potential on the need for aerenchyma tissues may reduce at low temperatures when respiration and thus oxygen demand is low.

The mechanisms through which such adaptive traits help plants adapt to wetland habitats, especially under flooded conditions, have been carefully studied in ecophysiological experiments (as reviewed in Colmer & Voesenek, 2009; Voesenek & Bailey-Serres, 2015). However, there is no analysis on the potentially generic driving factors of these plant traits in wetlands under natural environmental conditions. Despite their dominant ecological role in enhancing wetland plants' survival, those wetland adaptive traits

are not yet included in the global plant functional trait databases, such as the TRY (Kattge et al., 2011), while we consider this essential for comprehensive analyses within the functional ecology context. Most studies so far have focused on the molecular and physiological regulation of specific traits in a limited comparison of species or genotypes (e.g. Konnerup & Pedersen, 2017; Winkel, Colmer, Ismail, & Pedersen, 2013). Comparative experiments or field studies have concentrated on comparisons of trait expression within the local species pool (Colmer, Pedersen, Wetson, & Flowers, 2013; Pedersen, Pulido, Rich, & Colmer, 2011). To our knowledge, no study exists relating the expression of these traits to driving factors or to different wetland types on regional to global scales. Such understanding on the potential drivers of wetland adaptive traits comprises a fundamental step in applying trait-based approaches to wetland ecology.

In this research, we hypothesize that (a) bioclimatic variables, hydrological regime, habitat type and plant life-form, including their interactions, are potential key driving factors for wetland adaptive traits; (b) since wetland adaptive traits all respond and adapt to the adverse wetland conditions, we expect that the driving factors for different wetland adaptive traits are similar. We aim to assess and evaluate the importance of these driving factors in determining wetland adaptive traits. Using a newly compiled wetland plant adaptive trait dataset, our paper is the first exploration of various potential driving factors for three key wetland plant adaptive traits (root porosity, root/shoot ratio and underwater photosynthetic rate) that represent key plant strategies in response to adverse wetland conditions (including anoxia, flooding and submergence). As a fundamental step towards understanding the wetland plants' adaptive strategies, our results should reveal a new perspective on the driving factors for wetland adaptive traits in the broad context of functional ecology, and provide a benchmark for modelling and predicting wetland plant species distributions and their impacts on ecosystem functioning.

2 | MATERIALS AND METHODS

2.1 | Data compilation

We compiled a dataset of wetland plant adaptive traits, defining wetlands and wetland plants according to the Ramsar Convention (Ramsar Convention Secretariat, 2013), which includes plant species inhabiting aquatic systems (e.g. rivers and lakes) as well as those non-wetland terrestrial plants that inhabit temporarily/permanently flooded areas. The wetland plant adaptive trait dataset was compiled from a systematic search in Web of Science and Google Scholar (last updated on the 5 June 2018). The literature search included permutations of the following keywords: wetland plants, marsh plant, bog plant, isoetid, aquatic plants, macrophytes, submerged plants, floating-leaved plants, emergent plants, root porosity, root/shoot ratio and underwater photosynthesis. We also drew on references presented in several important reviews that focused on the ecophysiological studies of how wetland plants adapt to flooding conditions published in the past 15 years (e.g. Bailey-Serres & Voesenek, 2008; Voesenek & Bailey-Serres, 2015; Voesenek et al., 2006). Finally, we added several of our own unpublished data sources, along with others within our network.

For the current analysis, we selected those studies that (a) measured plants occurring in wetlands with sufficient information for us to consistently classify the habitat types and the hydrological regime(s) (drained, waterlogged or submerged); (b) were measured using field-collected specimens, thus we did not include data on plants from greenhouse experiments; and (c) provided accurate location information (with coordinates). We then compiled data from the selected studies that included quantitative measurements of three intensively studied wetland plant adaptive traits (root porosity [%], root/shoot ratio and the rate of underwater photosynthesis [mol m^{-2} s^{-1}]). We are aware that there are many other important wetland adaptive traits, such as root ROL, ethanol metabolism and tolerance of reduced metal ions. However, the data available for these traits either were measurements in greenhouse/laboratory settings or were available only in a qualitative form, which was not suitable for this quantitative analysis. In total, 598 trait records from 21 studies at 38 different study sites were analysed. For root porosity, the data comprised 198 measurements of 103 unique species in 13 studies at 25 different sites; root/shoot ratio data contained 321 measurements on 12 unique species, described in six studies at seven different sites; the 79 underwater photosynthetic rate measurements on 27 unique species were contained in three studies at eight different sites. Location of the sampling sites in a global map were shown in Appendix S2, Figure S1.

We included bioclimatic variables, hydrological regime, habitat type and the plant life-form (see Table 1) as potential drivers for the above-selected wetland plant adaptive traits. We could not include other abiotic variables, such as redox potential, due to a limited data availability and inconsistent measurement methods. Nevertheless, we believe that the variables we included, such as the hydrological regime, act as a good proxy for redox potential and oxygen depletion. We did not include soil variables in our

TABLE 1 The explanatory variables in the model as driving factors for wetland adaptation traits

Explanatory variables	Continuous/categories
Bioclimatic variables	temperature; precipitation
Hydrological regime	drained; waterlogged; submerged
Habitat type	fens; permanent forested wetlands; mangrove swamps; marshes; permanent brackish/saline non-forested wetlands; rivers and lakes; temporary brackish/saline non-forested wetlands; temporary non-forested wetlands
Plant life-form	emergent; floating-leaved; grass; isoetid; sedge; shrub/tree; submerged

analysis either. Local soil conditions in wetlands strongly deviate from those in nearby non-wetland terrestrial systems (organic matter content as an example) that is represented in available global soil databases. Also, the soil information provided in the original publications was inconsistent and insufficiently detailed to be included in our analyses.

For our analyses, we classified hydrological regime as drained, waterlogged or submerged (as defined by Sasidharan et al., 2017), as provided in the original study. While this provides baseline information on local (hydrological and fertility) wetland conditions, additional insights can be obtained from a classification into specific wetland habitat types. Based on the guidance of the Ramsar Convention (Ramsar Convention Secretariat, 2013) and the definitions by the Environmental Protection Agency (https://www.epa.gov/wetlands/classification-and-types-wetlands#marshes), we grouped wetland habitats into 11 categories (Appendix S1). Studies selected for the current paper encompassed eight habitat types (Table 1). We grouped the life-form of plants into seven categories (Table 1). We acquired bioclimatic variables at the global scale with an accuracy of 2.5 min (WorldClim Version 2.0, http://www.worldclim.org/; Fick & Hijmans, 2017). These bioclimatic variables represent 19 climate attributes of ecological importance, in terms of annual means, seasonality and extreme or limiting climate factors. To determine the major axes of variation in all bioclimatic variables and to minimize the effect of inter-correlations, we ran a principal component analysis (PCA), and took the scores of the first two axes of the PCA to represent the climatic conditions. The PCA surface and axis scores reveal that the first and second axes (explained 51.8% and 25.8% of total variance respectively) are mainly related to temperature and precipitation respectively (Appendix S2, Figure S2). Therefore, below we will refer these axes as *temperature* and *precipitation* respectively. Our data points represent most of the global bioclimatic space, illustrated by an overlay of the sampling points onto the PCA surface (Appendix S2, Figure S3).

2.2 | Data analysis

We constructed single-trait linear regression models to elucidate the role of variables in driving the three wetland plant adaptive traits. We used trait values recorded at the individual plant level. In some papers, measurements were summarized as a species $M \pm SD$, in which case we simulated the original number of data points (recorded sample size) based on a normal distribution around the recorded mean and standard deviation. The response variables were $\log_{10}$-transformed to approximate normality and logit-transformed in the case of root porosity (Warton & Hui, 2011).

For the root porosity trait, we included all four sets of explanatory variables—bioclimatic variables, hydrological regime, habitat type and plant life-form. Due to the limited data available for some of the combinations of categorical variables, we could add only the two-way interaction terms between the (continuous) bioclimatic variables and each of the three categorical variables. The full model for root porosity was therefore structured as:

$$\begin{aligned}\log_{10}(\text{Root porosity}/(1-\text{Root porosity})) &\sim \text{Temperature} + \text{Precipitation} \\ &+ \text{Hydrology} + \text{Habitat} + \text{Life-form} \\ &+ \text{Temperature:Hydrology} + \text{Precipitation:Hydrology} \\ &+ \text{Temperature:Habitat} + \text{Precipitation:Habitat} \\ &+ \text{Temperature:Life-form} + \text{Precipitation:Life-form} \\ &+ \text{Temperature:Precipitation}.\end{aligned}$$

Some of the study sites were geographically clustered, which might significantly affect the results. Given that we aimed to provide estimates of impacts of each driving factor, we were not interested in solving this clustering by including study sites as a random factor. Instead, after checking the amount of data available for each location, we randomly selected up to five measurements at each pixel (one pixel = 0.01 PCA score × 0.01 PCA score square cell) on the bioclimatic PCA surface (if there were fewer than five measurements, we included all the measurements) to maintain a balanced data structure for linear model construction.

We constructed the full model with the dataset as generated by the above-mentioned resampling process. For each resampled dataset, we ran a model selection on the full model based on the Akaike information criterion weight (AIC weight). For some resampled datasets, some coefficients could not be estimated because a combination of variables was—coincidently—not sampled. We excluded candidate models with such undefined coefficients, and rescaled the AIC weight for the remaining candidate models to sum to 1. This resampling and model selection was repeated 1,000 times.

Then we calculated the averaged AIC weight for each candidate model across all 1,000 iterations, and the best model was selected as being the candidate model with the highest averaged AIC weight (Burnham & Anderson, 1998). To gain a robust parameter estimation for the best model, we calculated the average adjusted R^2, average coefficient values of the intercept and each variable, and the average relative importance of each main effect based on the model parameters generated in all 1,000 iterations.

The root/shoot ratio had similar and even stronger data limitations in the categorical variables. Hence, we included only the main effects of the four set of variables—bioclimatic variables, hydrological regime, habitat type and plant life-form without interaction terms. The full model for root/shoot ratio was therefore:

$$\begin{aligned}\log_{10}(\text{Root/shoot ratio}) &\sim \text{Temperature} + \text{Precipitation} \\ &+ \text{Hydrology} + \text{Habitat} + \text{Life-form}.\end{aligned}$$

For this response variable, there was only one record in the habitat type 'mangrove swamp', which we excluded from further analysis. Following the same resampling approach as described above, we selected the best model and obtained its parameter estimates.

For the underwater photosynthetic rate, data were limited to three studies (see Appendix S2, Figures S1 and S3). Since these data were reasonably balanced across geographical space, we ran this linear model on the original data (without resampling). All data records were from within one habitat type (rivers and lakes) and one hydrological regime (submerged). We therefore used only bioclimatic variables, plant life-form and the interactions between them to construct the linear model. Thus, the full model for underwater photosynthetic rate is:

$$\log_{10}(\text{Underwater photosynthetic rate}) \sim \text{Temperature} \times \text{Precipitation} \times \text{Life-form}.$$

The analyses were performed in the R language (R Core Team, 2018). We used the dredge() function in the MuMIn package (Barton, 2018) to simplify the full model and obtain the AIC weight based on AICs values. We visually assessed whether the most assumptions were met. We then calculated the relative importance of the main effects in the best models by using the calc.relimp() function in the relimpo package (Grömping, 2006). To compare the trait variances between different functional group and habitat conditions, we ran Tukey's honest significant difference test (TukeyHSD) using glht() function in the multcomp package (Hothorn, Bretz, & Westfall, 2008).

3 | RESULTS

3.1 | Quantifying the driving factors for root porosity

The best model for root porosity included hydrological regime, temperature and the interaction term between them (Table 2; averaged adjusted R^2 = .42). Root porosity was overall positively correlated with temperature. Higher temperature conditions corresponded with a higher root porosity under drained and waterlogged conditions. Under submerged conditions, however, the impacts of temperature were rather weak (Figure 1). In our best model, the interaction term had the highest variance explained (17%) in comparison to hydrological regime (13%) and temperature (11%; Figure 4). Post-hoc comparisons suggested that the root porosity in submerged conditions was significantly higher than in waterlogged and drained conditions, while no significant difference was detected between waterlogged and drained conditions. Without the interaction term between temperature and hydrological regime, the best model would have included only habitat as the explanatory variable (see Table 2). This suggests that habitat type contains part of the underlying information as related to the hydrological conditions and temperature.

3.2 | Quantifying the driving factors for root/shoot ratio trait

The best model for root/shoot ratio included temperature, precipitation and habitat type (Table 2; averaged adjusted R^2 = .57). Habitat type played the most important role in determining the root/shoot ratio (explaining 26% of the variance; Figure 4). At higher temperatures, the root/shoot ratio was lower (Figure 2), which indicates that in a warmer environment relatively more biomass is allocated to shoots (explaining 16% of the variance). The root/shoot ratio was also positively correlated with precipitation (explaining 15% of the variance). This suggests that at higher

TABLE 2 Summary of the top five models fit to explain root porosity, root/shoot ratio and underwater photosynthetic rate respectively. The models were ranked based on the averaged Akaike information criterion (AIC) weight, which was calculated for each candidate model as the average AIC weight across 1,000 iterations. Proportion variance explained (average adjusted R^2) for the top models are also displayed

Wetland adaptive trait	Top models	Averaged AIC weight	Rank	Adjusted R^2
Root porosity	~Temperature × Hydrology	0.219	1	.42
	~Temperature × Hydrology + Precipitation	0.097	2	
	~Temperature + Precipitation + Habitat	0.059	3	
	~Precipitation + Habitat + Life-form	0.054	4	
	~Habitat	0.052	5	
Root/shoot ratio	~Temperature + Precipitation + Habitat	0.346	1	.57
	~Temperature + Precipitation + Habitat + Life-form	0.136	2	
	~Hydrology + Habitat	0.131	3	
	~Hydrology	0.064	4	
	~Life-form	0.040	5	
Underwater photosynthetic rate	~Precipitation + Life-form	0.245	1	.41
	~Temperature × Precipitation + Life-form	0.196	2	
	~Temperature + Precipitation + Life-form	0.128	3	
	~Precipitation × Life-form	0.112	4	
	~Temperature × Life-form + Precipitation × Life-form	0.080	5	

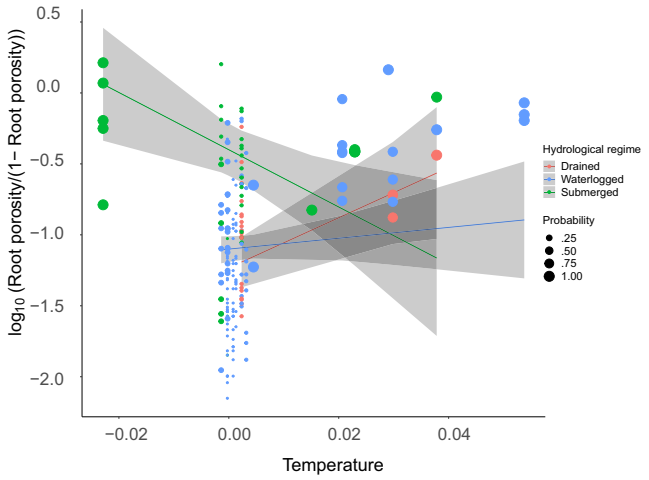

FIGURE 1 The relationship between logit-transformed root porosity and temperature grouped by different hydrological regime. The regression line and the 95% confidence interval are obtained by taking the mean of the bootstrapped parameters of the best model for 1,000 iterations, taking into account the biased spatial spread of the original data points. The bubble size indicates the sampling probability of each point in order to maintain a balanced spatial data structure (see details in Section 2)

precipitation, more biomass is allocated to roots. Hydrological regime was potentially important driving factors, which could partially replace the explanatory power of bioclimatic variables. The second best model suggests that the root/shoot ratio varied across different plant life-forms (Table 2).

3.3 | Quantifying the driving factors for underwater photosynthetic rate

The best model for underwater photosynthetic rate included precipitation and the plant life-form (Table 2; adjusted R^2 = .41). The precipitation-related bioclimatic variables positively affected underwater photosynthetic rate (Figure 3), explaining 22% of the variance (Figure 4). Plant life-form explained 19% of the variance. The TukeyHSD test suggested that the submerged leaves of floating-leaved plants had a significantly higher underwater photosynthetic rate compared to the submerged leaves of emergent and grass life-forms. This indicates a major advantage of floating-leaved plants over emergent plants and grasses in deep water.

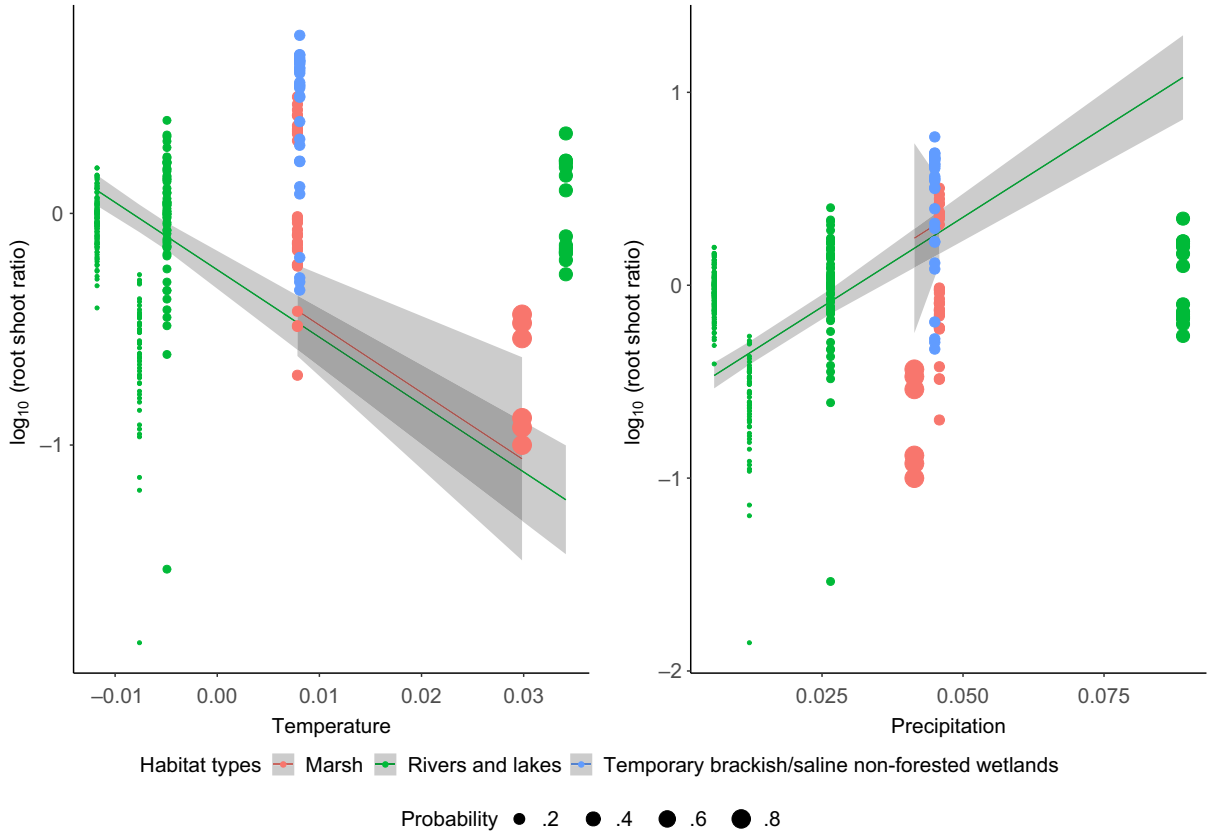

FIGURE 2 The relationship between $\log_{10}$-transformed root/shoot ratio and the bioclimatic variables (temperature left, precipitation right) grouped by different habitat types. The regression line and the 95% confidence interval were obtained by taking the mean parameters of the best model across 1,000 resampled dataset, taking into account spatial bias in the original data points (see Section 2). Regression lines represent marginal estimates and include the mean value of the other variable(s) in the model. Points indicate observed values. We note the lack of an environmental gradient in the data from temporary brackish/saline non-forested wetlands, and the overall interaction effects may therefore have been underestimated. The bubble size indicates the sampling probability of each point in order to maintain a balanced spatial data structure (see details in Section 2)

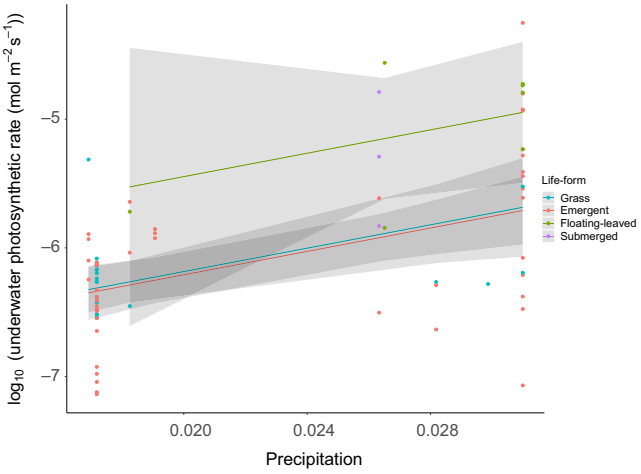

FIGURE 3 The relationship between $\log_{10}$-transformed underwater photosynthetic rate and precipitation grouped by different plant life-forms, as estimated by the top-ranked model

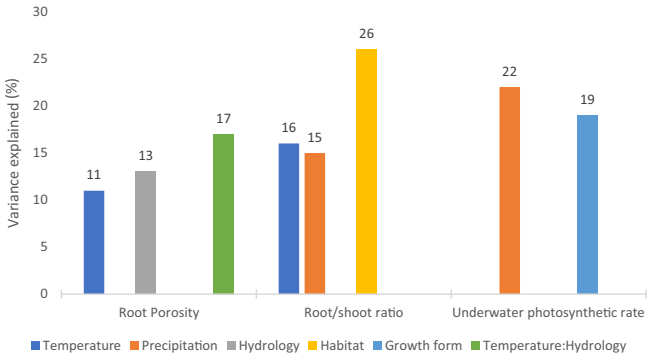

FIGURE 4 The contribution of each driving factor to the three wetland adaptive traits under study, as determined from the top-ranked models of each wetland adaptive trait

4 | DISCUSSION

The ecophysiology of wetland adaptive traits has been relatively well-studied, but the majority of this research has been limited to a small set of species under experimental conditions. A global analysis of the driving factors for wetland adaptive traits under natural environmental conditions is still missing. Using our newly compiled comprehensive wetland plant adaptive trait dataset, we explored the potential driving factors of three important wetland plant adaptive traits (root porosity, root/shoot ratio and underwater photosynthetic rate). Our models explained a substantial amount of the variation in the data, and revealed the importance of bioclimatic variables for all three traits—but for each trait in combination with different other driving factors, suggesting the existence of a myriad of wetland plant adaptive strategies. While based on a relatively small dataset, our study is a pilot exploration of available data of these wetland traits and attempts to bring wetland adaptive traits to the functional ecology context.

Among the four driving factors tested, bioclimatic variables were selected for all three wetland plant adaptive traits. Previous studies in terrestrial systems have shown that climatic variables not only drive the habitat conditions, but also various functional traits including leaf economics spectrum (LES; Maire et al., 2015; van Ommen Kloeke, Douma, Ordoñez, Reich, & van Bodegom, 2012; Wright et al., 2005), size traits (Wright et al., 2017), plant life-form (Ordoñez et al., 2009) and fine-root traits (Freschet et al., 2017). Our results extend this consistent theme of climate impacts to a broader context, from plants in drier terrestrial ecosystems to wetlands. The importance of bioclimatic variables additionally implies that the functional structure of wetland plants can be further impacted in the context of global climate change. Besides the bioclimatic variables, we demonstrated that hydrological regime, habitat type and plant life-form affected root porosity, root/shoot ratio and underwater photosynthetic rate respectively (Figure 4).

When assessing the driving factors of the three wetland plant adaptive traits, we found that simple combinations of bioclimatic variables (expressed in PCA multivariate space), hydrological regime, habitat type and plant life-form explained a substantial proportion of the trait expression (adjusted R^2 values range from .41 to .57). This proportion is similar to the filtering of non-wetland terrestrial traits by environmental conditions (Domingues et al., 2016; Maire et al., 2015; Reich & Oleksyn, 2004; Wright et al., 2005, 2017). The different drivers identified for different traits (Figure 4) imply that the filtering mechanisms for wetland plant adaptive traits seem trait-specific, rather than related to a single driving factor selecting for all adaptive traits.

4.1 | Ecological interpretation of the patterns in individual traits

Root porosity was driven by the temperature-related axis of bioclimatic variables. A positive response was detected under drained and waterlogged conditions. In warm areas, a higher temperature corresponds to a higher metabolic activity of plants resulting in a higher oxygen demand for transpiration and evapotranspiration. In those conditions, wetland plants need to develop a higher root porosity to ensure sufficient oxygen supply. Moreover, the oxygen solubility is reduced with increasing water temperature, amplifying the need for more porous tissues within roots for oxygen transport at higher temperature. In extremely cold habitats such as tundra areas where the soil water is frequently frozen, high root porosity might not be favourable since it results in reduced mechanical support (Striker, Insausti, Grimoldi, & Vega, 2007). In our model, the effect of air temperature on root porosity was much reduced under submerged conditions. This can be explained by the high specific heat capacity of water. When growing in submerged conditions, the atmospheric temperature has a limited impact on roots, whose temperature will be determined by relatively stable water temperatures. This suggests that future ecological modelling studies should include water temperature as a predictor variable for especially those submerged wetland plant species, for example, using global database of lake surface temperatures (Sharma et al., 2015). The different impact

of temperature in different hydrological regimes (as represented by the interaction term between temperature and hydrological regime) was the most important selected driving factor in the model, indicating the importance of these stabilizing effects of water on the impact of air temperature. Without the inclusion of the interaction term in the model, the next-best model was represented by the single explanatory variable of habitat type. Habitat type (e.g. fens, forested/shrub wetlands, marshes) convey combined information regarding hydrological regime and climatic variables at each site. Previous greenhouse studies indicated a significant difference in root porosity between drained and waterlogged conditions (Justin & Armstrong, 1987). In our study, we did not detect such differences mainly because most variation in root porosity in our database occurred between species. Hence, the impacts of hydrological regime on intraspecific variation were not picked up in our analysis.

Root/shoot ratio was driven by both temperature-related and precipitation-related axes of bioclimatic variables. At high temperature, plants need more oxygen to support the higher metabolic rates (Pedersen et al., 2016). In this situation, it is advantageous for plants to maintain a lower root/shoot ratio, since this reduces the relative oxygen consumption in the root tissues, and at the same time, increases the gas transport from the atmosphere to the root system (van Bodegom et al., 2005). Moreover, higher metabolic rates will ensure a faster biomass production, that is the capability to produce more shoot tissues when required by dynamic wetland conditions, which in turn, further reduces the root/shoot ratio. When it comes to forests, it has been found that low temperature induces a higher proportion of root biomass in adaptation to low available nutrient supply and limited soil solution movement (Poorter et al., 2012; Reich et al., 2014). While a matching case study in wetland is still lacking, our results indicate a similar pattern may exist here, albeit associated with a different mechanism.

In terrestrial conditions, more precipitation usually leads to a decrease in root/shoot ratio with increasing precipitation (Poorter et al., 2012; Schenk & Jackson, 2002). In contrast, our model suggested an increase in root/shoot ratio with increasing precipitation. These contrasting patterns for non-wetland terrestrial and wetland environments are presumably related to the extent of water limitation—much less severe in the latter, and suggest potentially varying mechanisms driving biomass allocation between below-ground and above-ground tissues. In wetland systems, water excess through precipitation and associated changes to submergence leads to limitations in oxygen availability. In contrast, in non-wetland terrestrial ecosystems, precipitation alleviates the water limitation and allows plants to invest less in root tissues to acquire water.

The rate of underwater photosynthesis was also positively related to precipitation. This result agrees with a meta-analysis on the response of global terrestrial ecosystems to precipitation (Wu, Dijkstra, Koch, Peñuelas, & Hungate, 2011), although here the mechanism involved may be different. In our study, the impact of precipitation was stronger for underwater leaves of some life-forms (floating-leaved and grass) than those of others (emergent and submerged plants), as indicated by the confidence interval of each life-form in Figure 3. We speculate that wetland plants in areas with more precipitation generally are more adapted to frequent flooding events, and therefore have a higher underwater photosynthetic rate. Another potential explanation for this pattern is that temporal wetlands generally differentiate from non-temporal wetlands by maximum water depth and sediment materials. The strategy of plants in coping with seasonal floods is anaerobic dormancy (a reduction of metabolic rates), and therefore do not need to maintain an optimum photosynthetic rate when fully submerged (Voesenek et al., 2004). This reasoning should be confirmed by further studies, as it is currently based on relatively few observations.

Interestingly, for underwater photosynthetic rate, temperature was not selected in the top model. This contrasts with studies of terrestrial plants, where temperature is an important driver for photosynthesis (Wu et al., 2011; Yamori, Hikosaka, & Way, 2014). Again, the high-specific heat capacity of water compared to air, and resulting dampened temperature fluctuations in inundated conditions may explain the limited impact of air temperature on underwater photosynthetic rate. Inclusion of observations in tropical regions (the underwater photosynthesis studies included in our analysis were all from temperate regions) may reveal other trends, since warm atmospheric temperatures (e.g. as high as 38°C) can diminish the underwater photosynthetic rates of plants in shallow pools when the small volume of water heats up owing to solar radiation (Pedersen et al., 2016). We also found that underwater leaves of floating-leaved and submerged plants had on average a higher underwater photosynthetic rate than the underwater leaves of emergent and grass life-forms. Floating-leaved and submerged plants have evolved many traits (e.g. leaves with thinner cuticle, enhanced utility of HCO_3^-) in adapting to submerged conditions, which may help maintain underwater photosynthesis (Colmer et al., 2011; Iversen et al., 2019; Rascio, Cuccato, Dalla Vecchia, La Rocca, & Larcher, 1999). Many floating-leaved and submerged plants are also able to use the CO_2 from sediment to facilitate underwater photosynthesis (Colmer, 2003b; Singer, Eshel, Agami, & Beer, 1994; Winkel & Borum, 2009).

4.2 | Ecological implications

While bioclimatic drivers were important for all three adaptive traits, different combinations of drivers were identified for each wetland adaptive trait. We hypothesize that a variety of driving mechanisms affect the expression of different wetland adaptive traits on a global scale. We therefore expect to see a decoupled pattern between some of the wetland adaptive traits. Along with the evidence that some wetland adaptive traits tend to be orthogonal to LES traits (Pan et al., 2019), our current results support the idea that these three (and potentially others as well) wetland adaptive traits are relatively cheap to develop, and therefore are not to a large-extent constrained by other adaptive traits or by LES traits.

Wetland adaptive traits are the premise of survival under the adverse conditions present in wetlands (Moor et al., 2017; Pan et al.,

2019; Voesenek & Bailey-Serres, 2015). The identified environmental filters in wetlands select plants with suitable adaptive traits, along with other factors including soil fertility, light radiation, competition/facilitation in communities (Luo et al., 2016). Disentangling the driving factors for wetland adaptive traits not only provides a theoretical basis for understanding the overall wetland plant functioning and strategy, but also creates new perspectives on modelling global wetland plant distributions and community structure (Lenssen, Menting, Van der Putten, & Blom, 2000; Visser, Bögemann, Van De Steeg, Pierik, & Blom, 2000; Willby, Pulford, & Flowers, 2001). These results can be included in GVMs (van Bodegom, Douma, & Verheijen, 2014; van Bodegom et al., 2012), which can in turn contribute to a better prediction of ecosystem processes such as those related to carbon, nitrogen and water cycles. For example, current global methane models, such as CLM4Me and LPJ-WHyMe, have considered the effect of plants only to constant plant functional type parameters (Riley et al., 2011; Wania, Ross, & Prentice, 2010). The results of this study may improve global methane model accuracy by quantifying the continuous trait expression on the varying environmental gradients.

Our study has shown that bioclimatic variables explain a great deal of variation in wetland plant functional traits on a global scale; however, our analysis was limited by the number of species, sites, variables and traits studied. Future studies should seek to expand the dataset that we have developed, which is freely available (see Data Accessibility Statement) and curated by the correspondence author. Many of the traits are relatively cheap to measure. Therefore, contributions of only a few days of work by a global network of wetland scientists would easily and greatly expand the database as a common resource for all.

5 | CONCLUSIONS

Understanding the potential drivers of wetland adaptive traits is a fundamental step towards future studies on wetland adaptive strategies and provides a reference for ecological modelling of wetland plants' distributions. Among the drivers we tested, bioclimatic variables are important driving factors for all three wetland plant adaptive traits. This finding extends the climatic variables as universal drivers of trait expression from non-wetland terrestrial ecosystems to wetlands. Perhaps more importantly, we show different drivers for different adaptive traits, which implies that each adaptive trait is most appropriate for a specific set of wetland conditions, and that there is no one common set of traits that best succeed in wetland conditions. This also suggests that there is a multitude of wetland plant strategies with potentially varied ecological mechanisms involved. Therefore, future wetland plant studies should consider a more complete set of driving factors to effectively bring wetland adaptive traits into the broad context of functional ecology.

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AUTHORS' CONTRIBUTIONS

P.M.v.B. initialized this research. Y.P., P.M.v.B. and E.C. designed and planned the research, and wrote the first drafts of the manuscript that was further improved by inputs from all co-authors, and finalized by Y.P. Y.P. and P.M.v.B. compiled the data with inputs from all co-authors. Y.P. ran all analyses with inputs from all co-authors. All the authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data deposited in the Dryad Digital Repository https://doi.org/10.5061/dryad.7h44j0zqx (Pan et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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